OVARIOLE NUMBERS IN SCARABAEOIDEA (COLEOPTERA: LUCANIDAE, PASSALIDAE, SCARABAEIDAE)[1]

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ABSTRACT—Ovariole numbers were determined for 4 genera of Lucanidae, 4 genera of Passalidae, and 65 genera of Scarabaeidae. Lucanidae had ovariole numbers of 6-6 and 12-12; Passalidae had only 2 ovarioles in each ovary. The most common ovariole number in Scarabaeidae was 6-6. Ovariole numbers ranged from 1-0 in Scarabaeinae to 14-25 in each ovary in *Pleocoma*, thought to be a relict form. An ovariole number of 12-12 occurred in one or more genera of Dynastinae, Rutelinae, and Cetoniinae. Although ovariole numbers usually represent a derived condition associated with egg laying habits and special features of each species' biology, there is still considerable indication of relationships between the groups.

In 1961, Robertson published a summary paper dealing with ovariole numbers in Coleoptera which combined his original findings with those of previous workers. He reported that within 329 species in 45 families ovariole numbers varied from one to several hundred. Robertson mentioned the single ovariole characteristic of Scarabaeinae (Coprinae) but concluded that there was remarkable uniformity in ovariole number in the Scarabaeoidea which usually had 6 ovarioles in each ovary. His data, however, shows 12-12 ovarioles in Lucanidae and 2-2 ovarioles in Passalidae, based on observations of only one species in each family.

Halffter and Matthews (1966), attributed the extreme ovarian reduction found in Scarabaeinae to nidification behavior. They reported that a single ovary with one ovariole was also present in *Canthon virens* Mann. and in two species of *Onthophagus*.

There is considerable information in the literature concerning grasshoppers (Orthoptera) and *Drosophila* (Diptera) that ovariole number is controlled by genetic factors (Blackith and Blackith, 1969; Robertson, 1957; and Tessier, 1963). For example, Robertson (1957) found that artificial selection in a strain of *D. melanogaster* for low ovariole numbers led to about a 14% reduction; selection in the other direction increased ovariole number by more than 50% and was still increasing after 10 generations. There is also evidence that ovariole number in

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some species of grasshoppers may vary significantly in different parts of a wide range (Uvarov, 1966; Blackith and Blackith, 1969).

The possibility that ovariole number could prove to be a meristic character of evolutionary and taxonomic value was suggested by Robertson (1961) for the Coleoptera and by Balduf (1964) for the Heteroptera. With this in mind, the writers herein report an extensive survey of ovariole numbers in the superfamily Scarabaeoidea.

Materials and Methods

Most of the specimens used in this study were collected alive and were freshly dissected in 70% ethanol, with the aid of a binocular stereomicroscope, as described by Kamm and Ritcher (1972). Other specimens were dissected by removal of the elytra and incision of the dorsal body wall of the abdomen, followed by removal of the contents of the abdomen until only the female reproductive tract remained. A number of the larger specimens were dissected by removal of the abdomen, followed by transverse and lateral incisions with microscissors. The dorsal portion was then pulled back to expose the female reproductive organs.

Serial sections were made with a standard rotary microtome, after fixation of the ovaries in modified Bouin's solution, transfer to ethanol, staining with iron haematoxylin, and impregnation with paraffin.

Illustrations were made using either a camera lucida or squared ocular grid, with specimens submerged in ethanol.

Many specimens used in this study were collected at or near the Southwest Research Station of the American Museum of Natural History, near Portal, Arizona. Other material was obtained alive in Oregon, Idaho, New Mexico, California, Texas, and North Carolina or was sent preserved in fluid from Japan, Australia, and Russia.

Discussion

In the discussion which follows, the families and subfamilies of Lucanidae and Scarabaeidae are arranged according to Arnett (1968). The subfamilies of Passalidae are listed according to Reyes-Castillo (1970). Table 1 lists the species we examined, number of ovarioles found, variation (if any), number of specimens dissected, and the state (USA) or foreign country from which specimens of each species were obtained.

Lucanidae (Fig. 16): Ovariole numbers of 6-6 and 12-12 were found in this family. In this regard the family resembles many Scarabaeidae. An ovariole number of 6-6 was found in 1 species in each of the subfamilies Platycerinae and Aesalinae. An ovariole number of 12-12 was observed in one species in each of the subfamilies Sinodendroninae (Fig. 16) and Lucaninae. Robertson (1961), cited Stein (1847) as finding 12-12 ovarioles in *Dorcus parallelipipedus* L., which belongs to the subfamily Dorcinae.

Passalidae (Fig. 3): In 1973, Baker reported that 3 species of

Table 1. Ovariole numbers in Scarabaeoidea

Group and Species	Locality	Usual Number (left-right)	Variation (per side)	Specimens Examined
	Lucanidae			
Lucaninae				
Lucanus mazama (LeConte)	Arizona	12-12	——	1
Platycerinae				
Platycerus oregonensis Westw.	Oregon	6-6	none	3
Aesalinae				
Ceruchus striatus LeConte	Oregon	6-6	——	1
Sinodendrinae				
Sinodendron rugosum Mann.	Oregon	12-12	11-12	14
	Passalidae			
Aulacocyclinae				
Aulacocyclus errans (Blackl.)	Australia	2-2	none	2
Cylindricaulus patalis (Lewis)	Japan	2-2	none	3
Passalinae				
Proculini				
Verres furcilabris (Esch.)	Trinidad	2-2	——	1
Episphenoides australasicus Perch.	Australia	2-2	none	5
	Scarabaeidae			
Scarabaeinae				
Onthophagini				
Onthophagus browni Howden and Cartwright	Arizona	1-0	none	3
Onthophagus hecate (Panz.)	South Dakota	1-0	none	2
Onthophagus striatulus striatulus (Beauv.)	North Carolina	1-0	none	5
Onthophagus velutinus Horn	Arizona	1-0	none	4
Oniticellini				
Oniticellus californicus Horn	Oregon	1-0	none	2
Coprini				
Ateuchus histeroides (Web.)	North Carolina	1-0	none	4
Dichotomius colonicus (Say)	Arizona	1-0	none	4
Phanaeus quadridens (Say)	Arizona	1-0	none	3
Phanaeus vindex MacL.	Arizona	1-0	——	1
Copris arizonensis Schffr.	Arizona	1-0	——	1
Copris lecontei Matthews	Arizona	1-0	none	4
Scarabaeini				
Canthon indigaceus LeConte	Arizona	1-0	none	3
Canthon imitator Brown	Arizona	1-0	none	3
Canthon pilularius (L.)	South Dakota	1-0	none	2
Glaphyrocanthon viridis (Beauv.)	North Carolina	1-0	none	4
Aphodiinae				
Aegialiini				
Aegialia blanchardi Horn	Oregon	3-3	2-3	12

Table 1. (*Continued*)

Group and Species	Locality	Usual Number (left-right)	Variation (per side)	Specimens Examined
Aphodiini				
Aphodius fossor (L.)	Oregon	7-7	none	10
Aphodius distinctus (Mull)	Idaho	5-5	——	1
**Aphodius fimetarius* (L.)	Oregon	7-7	none	4
**Aphodius fimetarius* (L.)	Idaho	7-7	none	4
Aphodius coloradensis Horn	Arizona	5-5	4-5	6
Aphodius denticulatus Hald.	Oregon	5-5	none	7
Aphodius granarius (L.)	Oregon	5-5	5-6	18
Aphodius lividus (Oliv.)	Arizona	5-5	——	1
Aphodius fucosus complex	Idaho	6-6	none	2
Aphodius hirsutus Brown	Oregon	6-6	5-6	4
Aphodius haemorrhoidalis (L.)	Oregon	5-5	none	18
Xeropsammodius desertus Van D.	California	5-5	——	1
Eupariini				
Ataenius cognatus (LeConte)	New Mexico	3-3	none	3
Ataenius deserta Horn	New Mexico	3-3	——	1
Psammodiini				
Psammodius oregonensis Cartwr.	Oregon	3-3	2-3	13
Trichiorhyssemus riparius (Horn)	Arizona	2-2	none	5
Pleurophorus caesus (Creutz)	Oregon	2-2	none	5
Ochodaeinae				
Ochodaeus biarmatus LeConte	New Mexico	6-6	none	2
Ochodaeus praesidii Bates	Arizona	6-6	5-6	2
Ochodaeus simplex LeConte	Oregon	6-6	none	2
Pseudochodaeus estriatus (Sch.)	Oregon	6-6	5-6	10
Geotrupinae				
Geotrupini				
Geotrupes splendidus (Fab.)	North Carolina	6-6	none	2
Mycotrupes gagei 01. and Hub.	Florida	6-6	5-6	2
Peltotrupes profundus Howden	Florida	6-6	5-6	2
Lethrini				
Lethrus lebedevi Sem.	USSR	6 6	none	2
Bolboceratini				
Bolbocerás obesum (LeConte)	Oregon	6-6	none	2
Bolborhombus carinatus (Schffr.)	Arizona	6-6	5-6	2
**Eucanthus lazarus* (Fab.)	Arizona	6-6	6-7	5
Pleocominae				
Pleocoma crinita Linsley	Oregon	variable	14-19	5
Pleocoma dubitabilis Davis	Oregon	variable	15-20	10
Pleocoma fimbriata LeConte	Oregon	18-19	——	1
Pleocoma hirsuta Davis	California	16-17	——	1
Pleocoma minor Linsley	Oregon	variable	16-19	3
Pleocoma oregonensis Leach	Oregon	variable	16-19	2
Pleocoma simi Davis	Oregon	variable	18-25	4
Glaphyrinae				
Lichnanthe rathvoni LeConte	Oregon	6-6	none	12
Acanthocerinae				
Cloeotus globosus Say	North Carolina	6-6	——	1

* Species whose ovariole numbers were listed by Robertson (1961).

Table 1. (*Continued*)

Group and Species	Locality	Usual Number (left-right)	Variation (per side)	Specimens Examined
Troginae				
Glaresis clypeata Van Dyke	Oregon	4-4	3-4	7
Glaresis mendica Horn	Arizona	4-4	none	3
Omorgus suberosus (Fab.)	Texas	3-3	none	2
Omorgus rubricans (Rob.)	Texas	3-3	——	1
Omorgus carinatus (Loomis)	New Mexico	3-3	——	1
Omorgus monachus (Herbst)	Texas	3-3	none	2
Omorgus fuliginosus (Rob.)	Texas	3-3	——	1
Omorgus asper (LeConte)	Texas	3-3	none	3
Omorgus tesselatus (LeConte)	Arizona	3-3	——	1
Omorgus texanus (LeConte)	Texas	3-3	——	1
Omorgus scutellaris (Say)	New Mexico	3-3	——	1
Trox scaber (L.)	Oregon	6-6	——	1
Trox atrox LeConte	Oregon	6-6	none	6
Trox s. spinulosus Rob.	Texas	6-6	——	1
Trox foveicollis Harold	Texas	6-6	——	1
Trox frontera Vaurie	Texas	6-6	none	2
Trox sonorae LeConte	New Mexico, Arizona	6-6	none	3
Trox robinsoni Vaurie	Texas	6-6	none	5
Trox tuberculatus (DeG.)	Texas	6-6	none	2
Trox plicatus Rob.	Arizona	6-6	none	6
Trox variolatus Melsh.	Texas	6-6	none	3
Melolonthinae				
Sericini				
Serica curvata LeConte	Oregon	6-6	none	2
Serica falcata Dawson	Oregon	6-6	none	20
Serica sp.	California	6-6	none	2
Melolonthini				
Diplotaxis subangulata LeConte	Oregon	6-6	none	3
Diplotaxis brevicollis (LeConte)	Oregon	6-6	none	2
Diplotaxis chiricahuae Fall	Arizona	6-6	none	3
Diplotaxis boops Bates	Arizona	6-6	——	1
Phyllophaga anxia (LeConte)	Idaho	6-6	none	6
Phyllophaga mucorea (LeConte)	California	6-6	none	4
Phyllophaga falsa (LeConte)	New Mexico	6-6	none	4
Phyllophaga disparilis (Horn)	Arizona	6-6	——	1
Polyphylla decemlineata Say	Arizona	6-6	none	3
Thyce herfordi Casey	California	6-6	——	1
Pachydemini				
Phobetus mojavus Barrett	California	6-6	none	2
Phobetus c. cornatus LeConte	Oregon	6-6	none	2
Macrodactylini				
Macrodactylus uniformis Horn	Arizona	6-6	none	4
Dichelonyx validus sulcatus (LeConte)	Arizona	6-6	none	4
Dichelonyx validus vicinus (Fall)	Oregon	6-6	none	7
Hopliini				
Hoplia hirta LeConte	Oregon	6-6	——	1
Hoplia oregona LeConte	California	6-6	——	1

Table 1. (*Continued*)

Group and Species	Locality	Usual Number (left-right)	Variation (per side)	Specimens Examined
Rutelinae				
Anomalini				
Anomala hardyorum Potts	California	6-6	——	1
Anomala nimbosa Casey	Arizona	6-6	5-6	3
Anomala marginata (Fab.)	North Carolina	6-6	——	1
**Popillia japonica* Newman	North Carolina	6-6	6-6	6
Strigoderma arboricola (Fab.)	North Carolina	6-6	5-6	3
Rutelini				
Cotalpa consobrina Horn	Arizona	12-12	——	1
Macraspis lucida (01.)	Mexico	6-6	——	1
Paracotalpa deserta Saylor	California	9-9	7-9	5
Paracotalpa granicollis (Hald.)	Oregon	12-12	11-12	4
Pseudocotalpa guilianii Hardy	Nevada	6-6	none	4
Parastasia brevipes (LeConte)	North Carolina	6-6	none	4
Pelidnota punctata (L.)	North Carolina	6-6	none	4
Plusiotis beyeri Skinner	Arizona	6-6	none	2
Plusiotis gloriosa LeConte	Arizona	6-6	none	5
Plusiotis lecontei Horn	Arizona	6-6	——	1
Dynastinae				
Cyclocephalini				
Ancognatha manca LeConte	Arizona	6-6	none	2
Coscinocephalus cribrifrons (Schffr.)	Arizona	6-6	——	1
Cyclocephala dimidiata Burm.	Arizona	6-6	none	4
Cyclocephala hirta LeConte	Arizona	6-6	——	1
Dyscinctus obsoletus (LeConte)	New Mexico	6-6	none	2
Oryctini				
Anoplognatho dunnianus Riv.	Arizona	6-6	——	1
Bothynus gibbosus obsoletus LeConte	New Mexico	6-6	5-6	5
Cheiroplatys clunalis (LeConte)	Arizona	6-6	none	3
Strategus cessus LeConte	Arizona	6-6	none	2
Xyloryctes jamaciensis (Drwry)	Arizona	6-6	6-7	2
Dynastini				
Dynastes granti Horn	Arizona	6-6	——	1
Phileurini				
Phileurus illatus LeConte	New Mexico	6-6	——	1
Cetoniinae				
Gymnetini				
Cotinis mutabilis G. & P.	Arizona	12-12	11-14	4
Cetoniini				
Euphoria inda (L.)	Idaho	12-12	11-12	2
Euphoria testacea Casey	Arizona	12-12	9-12	6
Cremastocheilini				
Cremastocheilus armatus Walk.	Washington	6-6	none	5
Trichiini				
Osmoderma eremicola Knoch	Kentucky	12-12	——	1
Trichiotinis affinis (G. & P.)	North Carolina	6-6	5-6	2
Valgini				
Valgus canaliculatus (Fab.)	North Carolina	6-6	none	4

Pentalobus each had 2 ovarioles in each ovary. Reyes-Castillo and Ritcher (1973) found the same 2-2 condition in 11 other species of Passalidae, belonging to 8 genera and including representatives of both subfamilies. We have also found 2-2 ovarioles in several more passalids. (Table 1).

It appears from the above observations that an ovariole number of 2-2 is probably constant throughout the family. This is a further indication of the compactness and uniformity of the group (Ritcher, 1966). Each ovariole produces several large eggs in succession.

Scarabaeidae, Scarabaeinae (Fig. 4): Only a single ovary, with one ovariole on the left side, was found in all species examined. This condition is apparently the same for all members of the subfamily (Cooper, 1938; Srivastava, 1951; Robertson, 1961; Gupta and Kumar, 1963; and Edmonds, 1974) and is not known to occur in any other Scarabaeoidea. The single ovariole usually has from one to three conspicuous ova in various stages of development.

Scarabaeidae, Aphodiinae (Fig. 5, 7 and 18): A wide range of ovariole numbers was found in this group. Ovariole numbers of 2-2, 3-3, 5-5, 6-6, and 7-7 were encountered. In the tribe Aphodiini, ovariole numbers of 5-5, 6-6, and 7-7 were found. The tribes Aegialiini and Eupariini had 3-3 ovarioles. Ovariole numbers of 2-2 and 3-3 were found in the tribe Psammodiini. In each ovary, several or all of the ovarioles produce mature eggs at the same time.

Scarabaeidae, Ochodaeinae (Fig. 8): A 6-6 ovariole number was found in *Ochodaeus* and *Pseudochodaeus* (Carlson and Ritcher, 1974). Like in the Geotrupinae, there was evidence of a sequential development of ova with only one mature egg being produced at a time. Production of a mature egg appeared to alternate from one ovary to the other and probably rotates among the ovarioles of each ovary.

Scarabaeidae, Geotrupinae (Fig. 6 and 20): All 7 genera surveyed had a 6-6 ovariole number. The ovaries were very similar to those of the Ochodaeinae and had the same pattern of staggered, sequential egg development. The ovarioles were often difficult to count because some were very small and all were enclosed in a common sheath. This is why Williams (1945) was uncertain about the ovariole number of *Bolbocerosoma farctum* (Fab.) and *Eucanthus lazarus*. Robertson (1961) misquoted him and stated incorrectly that these species had ovariole numbers of 1 and 1 (1-2) respectively.

Scarabaeidae, Pleocominae (Fig. 1 and 2): Seven species of *Pleocoma* had from 14 to 25 ovarioles in each ovary. There was no usual number of ovarioles evident, contrary to Ritcher (1966) who reported 18 per side. Ten females of *P. dubitabilis* had ovariole numbers of 17-17, 19-20, 19-16, 18-16, 17-15, 17-16, 20-17, 20-17, 15-?, and 16-?.

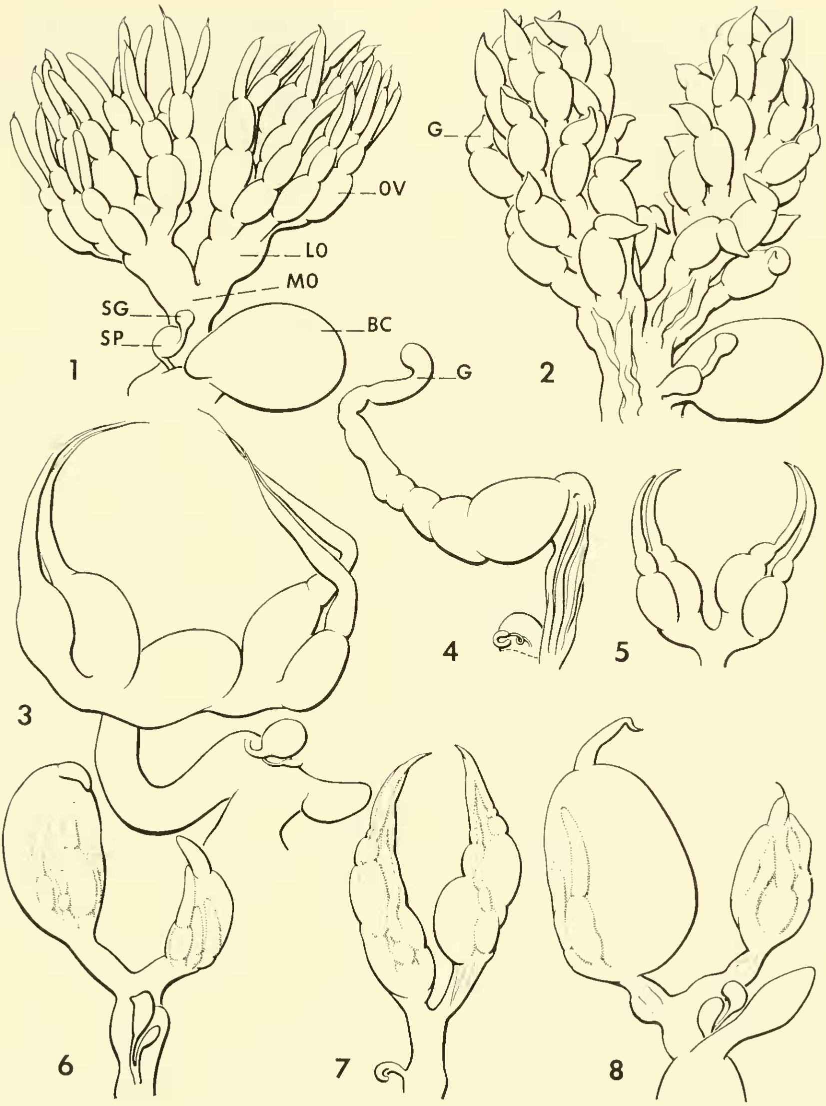

Fig. 1–8, dorsal views of female reproductive systems of Scarabaeoidea. 1, *Pleocoma dubitabilis* Davis. BC, bursa copulatrix; LO, lateral oviduct; MO, median oviduct; OV, ovariole; SG, spermathecal gland; SP, spermatheca. 2, *Pleocoma simi* Leach. G, *germarium*. 3, *Verres furcilabris* (Esch.). 4, *Oniticellus californicus* Horn, G, germarium. 5, *Trichorhyssemus riparius* (Horn) (spermatheca not shown). 6, *Bolboceras obesum* (LeC.). 7, *Aphodius granarius* (L.). 8, *Pseudochodaeus estriatus* (Schaeffer).

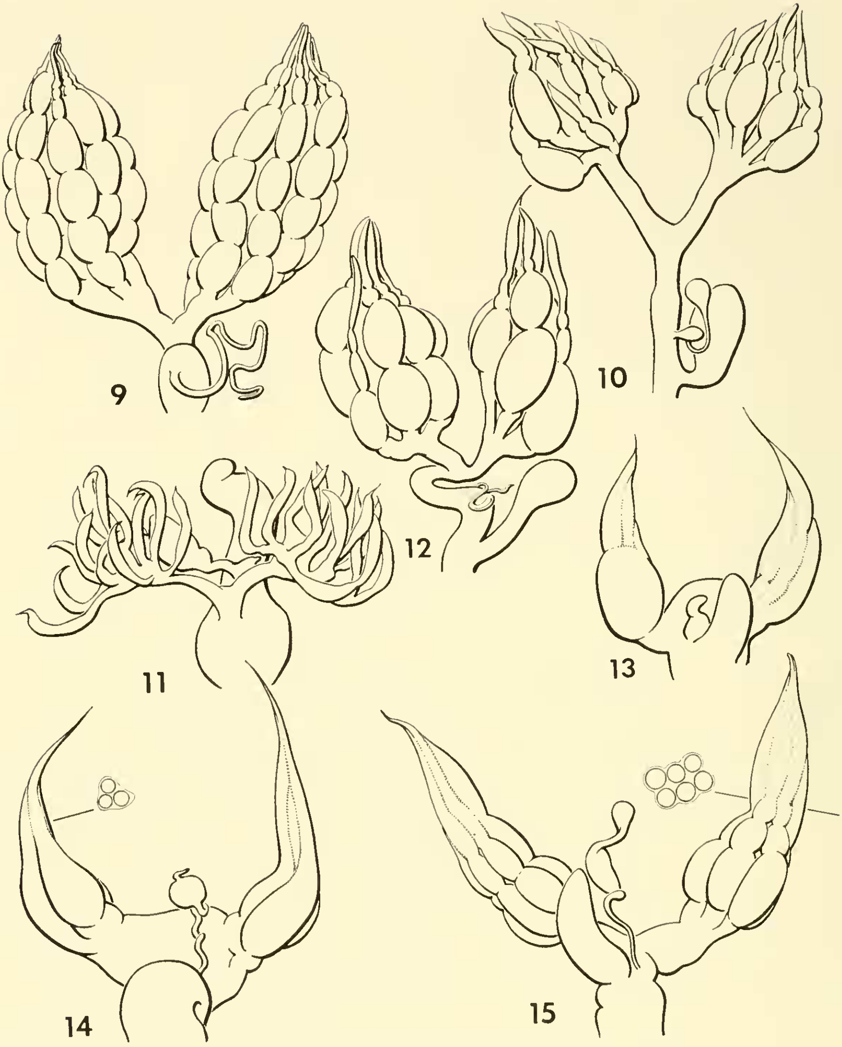

Fig. 9–15, female reproductive systems of Scarabaeoidea (all dorsal views except Fig. 11). 9, *Lichnanthe rathvoni* LeC.; 10, *Paracotalpa deserta* Saylor; 11, *Euphoria inda* (L.); 12, *Dichelonyx validus vicinus* Fall; 13, *Glaresis clypeata* Van Dyke; 14, *Omorgus scutellaris* Say; 15, *Trox atrox* LeC.

Five females of *P. crinita* had ovariole numbers of 14-19, 15-17, 18-18, 18-16, and 19-17. Each ovarian tubule in *Pleocoma* usually produces 1 or 2 eggs depending upon the size of the female (Fig. 1). In *P. simi*, however, each ovariole appears to produce only a single egg (Fig. 2).

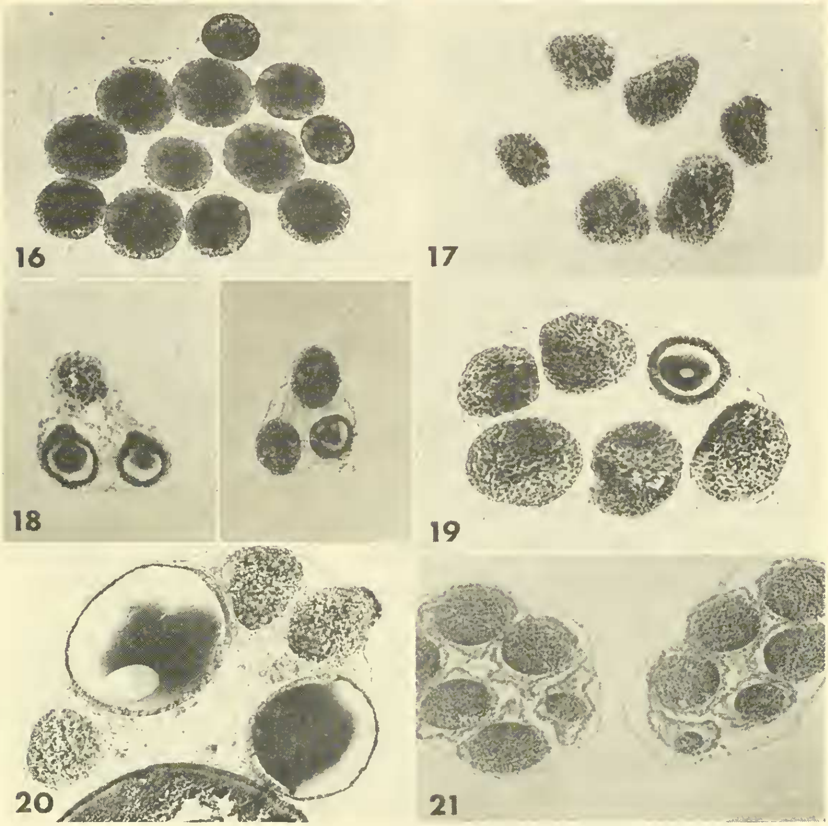

Fig. 16–21, cross sectional views of ovaries of Scarabaeoidea. 16, *Sinodendron rugosum* Mann.; 17, *Anomala hardyorum* Potts; 18, *Aegialia blanchardi* Horn; 19, *Dichelonyx validus vicinus* Fall; 20, *Geotrupes splendidus* (Fab.); 21, *Cloeotus globosus* Say.

All ovarioles produce mature eggs at approximately the same time and most of them are laid spirally in a single group (Ellertson and Ritcher, 1959).

In 6 of the 7 species of *Pleocoma* which were examined, the bases of the ovarioles in each ovary were attached to the short lateral oviduct at or near its apex (Fig. 1). In *P. simi*, ovaries were more elongate with the bases of many ovarioles attached along the sides of the lateral oviduct (Fig. 2).

Scarabaeidae, Glaphyrinae (Fig. 9): Females of *Lichnanthe* have 6-6 ovarioles which produce their eggs at the same time. Each ovariole had 6 or more well developed ova. (Fig. 9).

Scarabaeidae, Acanthocerinae (Fig. 21): *Cloeotus*, the only acanthocerine dissected, had 6-6 ovarioles, with the ova in each developing at the same time. It was necessary to make serial cross sections to be sure of the ovariole number since the ovarioles in each ovary were contained in a sheath (Fig. 21).

Scarbaeidae, Troginae (Fig. 13, 14, and 15): Each genus of this subfamily had a different ovariole number. The 3-3 number of *Omorgus* and the 6-6 number of *Trox* were first cited by Baker (1968) along with 16 additional characters to support the validity of *Omorgus* as a genus. Nine species of *Omorgus* had an ovariole number of 3-3 (Fig. 14) and ten species of *Trox* (*sensu strictu*) had an ovariole number of 6-6 (Fig. 15). No variation in number was encountered for any species of either genus.

Glaresis is the only genus of Scarabaeoidea known to have a 4-4 ovariole number. The female reproductive system resembles that of the Ochodaeinae and the Geotrupinae in that only one egg appears to develop at a time (Fig. 13).

Scarabaeidae, Melolonthinae (Fig. 12 and 19): Nine genera belonging to 5 tribes had an ovariole number of 6-6. There was simultaneous development of ova in all the ovarioles with each ovariole producing a number of eggs. Berberet and Helms (1972) gave an excellent account of the female reproductive system of *Phyllophaga anxia*. Menees (1963) found 6 ovarioles per side in *Amphimallon majalis* Razoum.

Scarabaeidae, Rutelinae (Fig. 10 and 17): Females of 5 genera of Anomalini all had 6-6 ovarioles. Females of 5 genera of Rutelini also had 6-6 ovarioles (Fig. 10). A sixth genus of Rutelini (*Cotalpa*) had 12-12 ovarioles. In a seventh genus of Rutelini (*Paracotalpa*) one species had 12-12 ovarioles and a second species had 9-9 (Fig. 10). Ova develop simultaneously in the ovarioles of the Rutelinae.

Scarabaeinae, Dynastinae: Eleven genera, belonging to 4 tribes, had 6-6 ovarioles. Gruner (1968), however, observed that *Phyllognathus silenus* F. (tribe Oryctini) usually had 11 or 12 ovarioles per side. Dissection of 323 ovaries indicated that the number of ovarioles ranged from 8–12. We found that each ovariole usually had 3 ova developing at the same time and all ovarioles were functional at the same time.

Scarabaeidae, Cetoniinae (Fig. 11): Two basic ovariole numbers were found in this group, 6-6 and 12-12. The 6-6 number was found in 3 species, each belonging to a different genus and each in a different tribe (*Cremastocheilini, Trichiini* and *Valgini*). The 12-12 number was found both in the Cetoniini (Fig. 11) and in the Trichiini.

Conclusions

Any conclusion as to the number of ovarioles in the ancestral form which gave rise to the Scarabaeoidea would be premature at this time. More information about ovariole numbers in the Dascilloidea, thought to be close relatives by Böving and Craighead (1931) and by Crowson (1960 and 1971), would be helpful.

This study suggests that the number of ovarioles in most forms studied represents a derived condition closely associated with egg laying habits and other peculiarities of each species' biology. The basic ovariole number in Scarabaeoidea appears to be 6-6. The fact that this number often occurs among both Lucanidae and Scarabaeidae indicates that the two families are closely related and much less closely related to the Passalidae. Subfamilies of the Scarabaeidae in which 6-6 ovarioles occur, without exception, are the Ochodaeinae, Geotrupinae, Acanthocerinae and Melolonthinae. The 6-6 number is also common in most Dynastinae, in many Rutelinae and Cetoniinae, in *Trox* and in several Aphodiinae.

Reductions from the 6-6 number of ovarioles are found in all Passalidae (2-2), some Troginae (3-3, 4-4), and most Aphodiinae (2-2, 3-3, 5-5).

In several subfamilies of Scarabaeidae where provisioning is the rule, 2 other kinds of reduction have occurred. In the Geotrupinae and Ochodaeinae the 6-6 ovariole condition still remains but only one egg is developed on each side at a time, with development alternating between the 2 ovaries. The most extreme reduction of the ovaries found in provisioners is found in the Scarabaeinae. They have lost all the ovarioles except for a single one on the left side.

The 12-12 ovariole number found in some Lucanidae, Rutelinae, Cetoniinae and at least one species of Dynastinae is difficult to explain since it is more common in genera considered more highly specialized. It is probably a secondary adaptation that has arisen independently several times by a doubling of the 6-6 number. The 9-9 number found in one species of Rutelinae probably represents a reduction from the 12-12 condition found in another species in the same genus (*Paracotalpa*).

The large, variable number of ovarioles found in *Pleocoma* may represent a primitive rather than a specialized condition. If so, this is one more bit of evidence that *Pleocoma* is a relict form.

The Passalidae are quite different in many respects from the other Scarabaeoidea (Ritcher, 1969) and appear to be quite specialized by possessing only two ovarioles per side. This same number seems to be characteristic for the whole family since examination of a number of genera has shown no deviation.

In groups with few ovarioles, either only a few large eggs develop per individual or each ovariole produces a comparatively large number of eggs. In *Pleocoma* which has a large number of ovarioles, each of the ovarioles produces only 1 or 2 eggs in some species and only 1 egg in at least one species (*P. simi*).

In *Glaresis*, *Cloeotus*, Geotrupinae, and Ochodaeinae, each ovary has an outer sheath which makes it difficult to determine the number of ovarioles. In many other Scarabaeidae, immature ovaries are also enveloped in a sheath early in their development. Later, as the ovarioles develop, however, the sheath disappears leaving the ovarian tubules distinctly separated (Berberet and Helms, 1972). In some Cetoniinae, the ovarioles are distinctly separated even in the immature ovaries of newly transformed adults.

Generally the number of ovarioles was quite constant in species with 7 or fewer ovarioles in each ovary. Species with 6-6 ovarioles occasionally had 5 or 7 on one side, those with 5-5 occasionally had 4 or 6. In some species having 12-12 ovarioles, such as *Sinodendron rugosum*, one ovary with 11 ovarioles occurs infrequently. Several cetoniine species having 12-12 ovarioles had a variation of from 9 to 14 ovarioles. In *Pleocoma*, which had the largest number of ovarioles, there was no usual number. Ten *P. dubitabilis* females, had from 15 to 20 ovarioles in each ovary with an average number of 17.2.

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References

Arnett, R. H. Jr. 1968. The beetles of the United States (a manual for identification). Amer. Entomol. Inst., Ann Arbor, Mich., U.S.A. 1112 p.

Baker, C. W. 1968. Larval taxonomy of the Troginae in North America with notes on biologies and life histories (Coleoptera: Scarabaeidae). USNM Bull. 279:1–79.

Baker, W. V. 1973. The genitalia of three species of *Pentalobus* (Col: Passalidae). J. Nat. Hist. 7:435–440.

Balduf, W. W. 1964. Numbers of ovarioles in the heteroptera. Proc. Entomol. Soc. Wash. 66(1):2–5.

Berberet, R. C. and T. J. Helms. 1972. Comparative anatomy and histology of selected systems in larval and adult *Phyllophaga anxia* (Coleoptera: Scarabaeidae). Ann. Entomol. Soc. Amer. 65(5):1026–1053.

Blackith, R. E. and R. M. Blackith. 1969. Variation of shape and of discrete anatomical characters in the morabine grasshoppers. Aust. J. Zool. 17:697–718.

Böving, A. G. and F. C. Craighead. 1931. An illustrated synopsis of the principal larval forms of the order Coleoptera. Entomol. Amer. 11(N.S.)(1–4): 1–351.

Carlson, D. C. and P. O. Ritcher. 1974. A new genus of Ochodaeinae and a description of the larva of *Pseudochodaeus estriatus* (Schaeffer). Pan-Pac. Entomol. 50(2):98–109.

Cooper, R. H. 1938. Notes on the internal anatomy of *Canthon laevis* (Coleop.: Scarab.). Iowa St. Coll. J. Sci. 12:461–466.

Crowson, R. A. 1960. The phylogeny of Coleoptera. Annual Rev. of Entomol. 5:111–134.

————. 1971. Observations on the superfamily Dascilloidea (Coleoptera: Polyphaga). With the inclusion of Karumiidae and Rhipiceridae. Zool. Jr. of the Linn. Soc. 50(1):11–19.

Edmonds, W. D. 1974. Internal anatomy of *Coprophanaeus lancifer* (L.). Int. J. Insect Morph. and Embryol. 3. In Press.

Ellertson, F. E. and P. O. Ritcher. 1959. Biology of rain beetles, *Pleocoma* spp., associated with fruit trees in Wasco and Hood River counties, Oregon. Agr. Expt. Sta. Tech. Bull. 44:1–42.

Gruner, L. 1968. Contribution a l'étude de l'ovogenèse d'un dynastide, *Phyllognathus silenus* F. essai préliminaire de chimiosterilisation. Ann. Epiphyties 19(2):267–304.

Gupta, A. K. D. and R. Kumar. 1963. Morphology and histology of the female reproductive organs of some beetles (Coleoptera). Indian J. of Entomol. 25(2): 147–160.

Halffter, G. and E. G. Matthews. 1966. The natural history of dung beetles of the subfamily Scarabaeinae (Coleoptera, Scarabaeidae). Folia Entomol. Mex. 12–14:1–312.

Kamm, J. A. and P. O. Ritcher. 1972. Rapid dissection of insects to determine ovariole development. Ann. Entomol. Soc. Amer. 65(1):271–274.

Menees, J. H. 1963. The embryonic and postembryonic homologies of insect genitalia as revealed in the development of the male and female reproductive systems of the European chafer, *Amphimallon majalis* Razoumowski (Coleoptera: Scarabaeidae). Cornell U. Memoir 381:1–59.

Reyes-Castillo, P. 1970. Coleoptera, Passalidae. Morfolgía y división en grandes grupes; géneros americanos. Folia Entomol. Mex. 20–22:1–240.

————, and P. O. Ritcher. 1973. Ovariole number in Passalidae (Coleoptera). Proc. Entomol. Soc. Wash. 75(4):478–479.

Ritcher, P. O. 1966. White grubs and their allies, a study of North American scarabaeoid larvae. Oregon State Univ. studies in Entomol. 4:1–219.

————. 1969. Morphology of the posterior procoxal bridges in Scarabaeoidea (Coleoptera). Coleopt. Bull. 23(4):89–92.

Robertson, F. W. 1957. Studies in quantitative inheritance. X. Genetic variation of ovary size in *Drosophila*. J. Genet. 55:410–443.

Robertson, J. G. 1961. Ovariole numbers in Coleoptera. Canad. J. of Zool. 39:245–263.

Srivastava, P. D. 1951. Occurrence of unpaired ovary in *Onitis distinctus* Lans. Curr. Sci., Bangalore 21:105.

Stein, F. 1847. Vergleichende Anatomie und Physiologie der Insekten. I. Die weiblichen Geschlechtsorgane der Käfer. Duncker und Humblot, Berlin.

Tessier, G. 1963. Evolution of the mean ovariole number in experimental populations of *Drosophila melanogaster*. Proc. 11th Entomol. Cong. Genet. 1:168 (Abstract).

Uvarov, B. P. 1966. Grasshoppers and locusts, a handbook of general acridology. 1:1–481. Cambridge Univ. Press.

Williams, J. L. 1945. The anatomy of the internal genitalia of some coleoptera. Proc. Entomol. Soc. Wash. 47(1):73–91.